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GYMNOSPERMS FROM THE MIDDLE TRIASSIC OF ANTARCTICA: THE FIRST STRUCTURALLY PRESERVED CYCAD POLLEN CONE

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The first permineralized cycad pollen cone is described from the lower Middle Triassic of Antarctica. The cone is characterized by helically arranged, wedge-shaped microsporophylls, each with five or more spinelike projections extending from the rhomboid distal face. The vascular cylinder is dissected and produces paired traces to each microsporophyll. Three vascular bundles enter the base of the microsporophyll and divide to produce at least five vascular strands in the sporophyll lamina. Pollen sacs occur in two radial clusters near the lateral margins on the abaxial surface of the microsporophyll. Each cluster bears up to eight elongate pollen sacs that are fused for approximately half their length and display longitudinal dehiscence. Pollen sacs are sessile and attached to a vascularized, receptacle-like pad of tissue that is raised from the surface of the microsporophyll. Pollen is ovoid, psilate, and monosulcate. Although the affinities of this cone with the Cycadales are obvious, the complement of characters in the fossil is unique and thus does not permit assignment to an extant family. Features of the cone are evaluated against reproductive aspects of living cycads.

Keywords: Cycadales, *Delemaya*, gymnosperms, microsporophylls, pollen cone.

Introduction

The Cycadales are a relict group that represent one of the most ancient lineages of seed plants, with a fossil record that extends >250 million years (Zhu and Du 1981). Cycads are thought to have originated in the Carboniferous and reached a zenith of diversity and distribution during the Mesozoic, yet their evolutionary history has remained relatively poorly understood (Norstog and Nicholls 1997; Jones 2002). In part, this results from the co-occurrence in the fossil record of foliage that is morphologically similar to that of cycads but represents other gymnosperm groups (e.g., pteridosperms and Bennettitales), which may be only distantly related. In addition, reproductive structures of fossil cycads, which could yield significant data to help clarify the relationships of early cycads with other groups of seed plants, are rare. There are descriptions of cycad megasporophylls and pollen cones from the Permian of China (Zhu and Du 1981; Wang 1986; Gao and Thomas 1989; Zhu et al. 1994); however, all fossil cones currently assigned to the Cycadales are compressions that display overall morphology but preserve few details of internal organization. This has hindered elucidation of the affinities of early members of this group. Their relationships relative to other fossil and modern seed plants continue to remain problematic, although modern cycads are recognized as monophyletic (Crane 1985; Nixon et al. 1994; Rothwell and Serbet 1994; Doyle 1996, 1998; Magallón and Sanderson 2002; Rydin et al. 2002). Because suitable fossil evidence of cycads has been scarce, many recent phylogenetic analyses have been based on molecular data, although there is growing recognition that this approach has not been particularly successful in resolving relationships among extant seed plants, particularly with respect to taxa with extensive evolutionary histories (Donoghue and Doyle 2000; Qiu et al. 2000; Sanderson and Doyle 2001; Magallón and Sanderson 2002; Rydin et al. 2002; Soltis et al. 2002; Thorne and Kishino 2002). It is clear that integrating information from the fossil record is essential for reconstructing the phylogeny of modern plants. Therefore, each fossil taxon that can unequivocally be assigned to the Cycadales provides a critical data point that can be used to fill gaps in our current understanding of the fossil record of this group.

Here, we provide the first description of an anatomically preserved cycad pollen cone from the early Mesozoic. This specimen is part of an early Middle Triassic flora from the Fremouw Peak locality in the central Transantarctic Mountains that contains a wealth of structurally preserved plants, including stems of the small-statured cycad *Antarcticycas schopfii* Smoot, Taylor et Delevoryas (Smoot et al. 1985). Anatomical and morphological features affiliate the cone with Cycadales; however, the complement of characters observed in the fossil is unlike any that exists in cycads today. These features are compared with pollen cones of both extinct and extant cycads, which offer a rare opportunity to consider possible systematic and biological implications of these reproductive organs in an early representative of this ancient group of seed plants.

Material and Methods

The pollen cone is preserved in permineralized peat collected from Fremouw Peak in the Queen Alexandra Range of the

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central Transantarctic Mountains (84°17′41″S, 164°21′48″E, 2385 m a.s.l.; Barrett and Elliot 1973). The age of the upper Fremouw Formation is early Middle Triassic, on the basis of palynostratigraphic analysis and vertebrate fossils (Farabee et al. 1990; Hammer et al. 1990). Polished surfaces were etched in 49% hydrofluoric acid, and specimens were studied by preparing cellulose acetate peels (Galtier and Phillips 1999). Peels were mounted on microscope slides, which are housed in the Paleobotany Division of the Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, under accession numbers 21434–21600 and 26026–26058.

For SEM, elevated wax wells were built directly around microsporophylls of interest on the surface of the silicified peat slab 11424 L_{top}, and *in situ* pollen grains were macerated using 49% hydrofluoric acid (Osborn and Taylor 1993). Macerated material was transferred into microcentrifuge tubes, rinsed in water and acetone, and then poured onto a microscope slide. Once the acetone evaporated, an SEM stub with sticky tape was lightly pressed over the slide to pick up the scattered material. Stubs were coated with palladium gold and viewed with a JEOL JSM-1600 at 6 kV.

Systematic Paleobotany

Order—*Cycadales*

Family—Incertae sedis

Genus—Delemaya *Klavins, Taylor, Krings et Taylor gen. nov.*

Generic diagnosis. Pollen cone simple, glabrous, elliptical in longitudinal section; vascular cylinder dissected into separate segments; tracheids annular to alternate pitted; microsporophylls helically arranged, imbricate, wedge shaped in longitudinal section, pentagonal in cross section, upturned tip forming rhomboid face with multiple projections directed toward cone apex; pollen sacs abaxial, in radial clusters, partially fused; pollen sac wall multilayered, dehiscence longitudinal; pollen ellipsoidal, monosulcate, psilate.

Type. *Delemaya spinulosa* sp. nov.

Delemaya spinulosa *Klavins, Taylor, Krings et Taylor sp. nov.*

(*Fig. 1; Fig. 2*A, *2*C–2E*; Fig. 3*A–*3*F)

Specific diagnosis. Cone at least 30 mm long; microsporophylls with three vascular bundles at base, at least five distally; at least five sharp-tipped projections at microsporophyll face, central projection longest; microsporophylls with two distinct radial clusters of pollen sacs separated by a sterile keel; each cluster with up to eight sessile pollen sacs on elevated, vascularized receptacular pad; spherical cortical cavity lacking contents at point of attachment of pollen sacs; pollen sacs elongate, up to 1 mm long and 0.5 mm wide, fused for up to half their length; pollen sac wall of two to three layers of thin-walled cells beneath distinct, thick-walled epidermis; wall thickness increases toward apex of pollen sac; pollen up to 20 μm long and 15 μm wide, sulcus smooth.

Derivation of name. The generic name *Delemaya* is proposed in honor of Ted Delevoryas and Sergius H. Mamay, both of whom have made highly significant contributions to our current understanding of the evolutionary history of cycads. The specific epithet *spinulosa* (Latin) refers to the small spines on the upturned distal tips of the microsporophylls.

Types. Holotype, 159 slides of specimen 11424 M_{bot}, slide numbers 21434–21438; 21440–21579; 26029–26048; fig. 1; fig. 2*A*, 2*C*–2*E*; fig. 3*A*–3*E*. Paratype, 35 slides of 11424 L_{top}, slide numbers 21438; 21580–21600; 26026–26028; 26049–26058; fig. 2*B*.

Repository. Division of Paleobotany, Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence.

Locality. Fremouw Peak, Queen Alexandra Range, Antarctica (84°17′41″S, 164°21′48″E, 2385 m a.s.l.), Buckley Island Quadrangle, Barrett and Elliott, 1973.

Stratigraphy. Upper portion of the Fremouw Formation.

Age. Early part of the Middle Triassic.

Description

The description that follows is on the basis of a pollen cone that occurs in close proximity to a stem of *Antarcticycas schopfii* but not in organic attachment. The cone is well preserved at the apex; however, the quality of preservation decreases toward the proximal end. Features described here are therefore primarily based on those observed in more apical microsporophylls. The cone is simple, glabrous, elliptical in longitudinal section, and at least 30 mm long and 8 mm wide (fig. 1*A*). Because the cone is small, no attempt was made to reorient the specimen by selective grinding to obtain a more median longitudinal section. The base of the cone is incomplete and therefore the total length could not be determined. Microsporophylls are wedge shaped in longitudinal section, helically arranged, and bear pollen sacs on the abaxial surface (fig. 1*A*). The apex of each microsporophyll is upturned, forming a rhomboid face with at least five elongate, sharp-tipped projections that extend toward the cone apex (fig. 2*B*). Pollen sacs are clustered into two separate radial clusters on each microsporophyll (fig. 2*A*), with up to eight pollen sacs per cluster (fig. 3*B*). Pollen sacs dehisce by a longitudinal slit (fig. 3*C*). Pollen is psilate, monosulcate, and ellipsoidal in outline (fig. 3*F*).

Cone Axis

The pith of the cone axis measures up to 1.1 mm in diameter and is composed of thick-walled, isodiametric cells that lack contents (fig. 1*B*). No secretory structures occur in the pith. A vascular cylinder that is dissected into multiple bundles surrounds the pith (fig. 1*B*). Each bundle consists of tracheids with annular to scalariform thickenings, or alternate pitting (fig. 1*B*). It is not possible to distinguish between protoxylem and metaxylem; secondary xylem is absent. Phloem cells are not preserved, although areas in which phloem probably occurred appear lighter in color. Traces to each microsporophyll are produced helically and originate as two bundles produced from the neighboring ends of two adjacent segments (sympodia) of the vascular cylinder in the cone axis. As the trace progresses through the cortex, one bundle dichotomizes so that

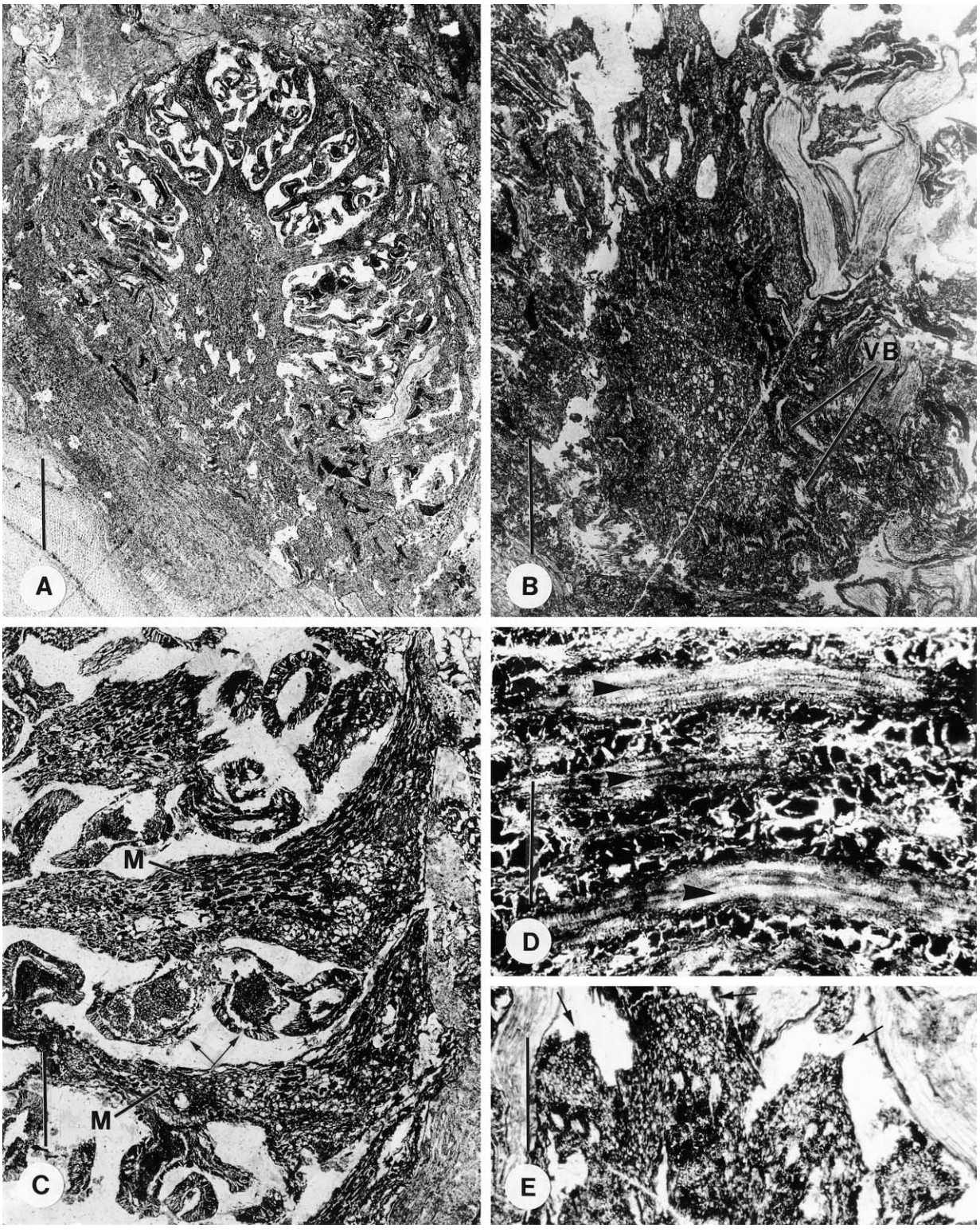

Fig. 1 *Delemaya spinulosa* gen. et sp. nov. *A*, Oblique longitudinal section through the apical region of the pollen cone. Note ring of cavities in the cortex of the cone axis. Scale bar = 2 mm. Slide 21434; 10424 M_{bot}, number 115. *B*, Oblique cross section through the cone axis showing pith and dissected bundles (*VB*) of the vascular cylinder. Scale bar = 1 mm. Slide 21435; 10424 M_{bot}, number 42. *C*, Longitudinal section through two microsporophylls (*M*) with clusters of pollen sacs (arrows) attached approximately midway along the microsporophylls. Note elongate, sharp-tipped projections at the distal face (right side). Scale bar = 500 μm. Slide 21434; 10424 M_{bot}, number 115. *D*, Longitudinal section of a microsporophyll trace with three vascular bundles (arrowheads) comprised of scalariform tracheids. Scale bar = 10 μm. Slide 21436; 10424 M_{bot}, number 92. *E*, Cross section through the bases of three microsporophylls (arrows) attached to the cone axis; each has three light areas corresponding to the position of vascular bundles. Scale bar = 500 μm. Slide 21437; 10424 M_{bot}, number 18.

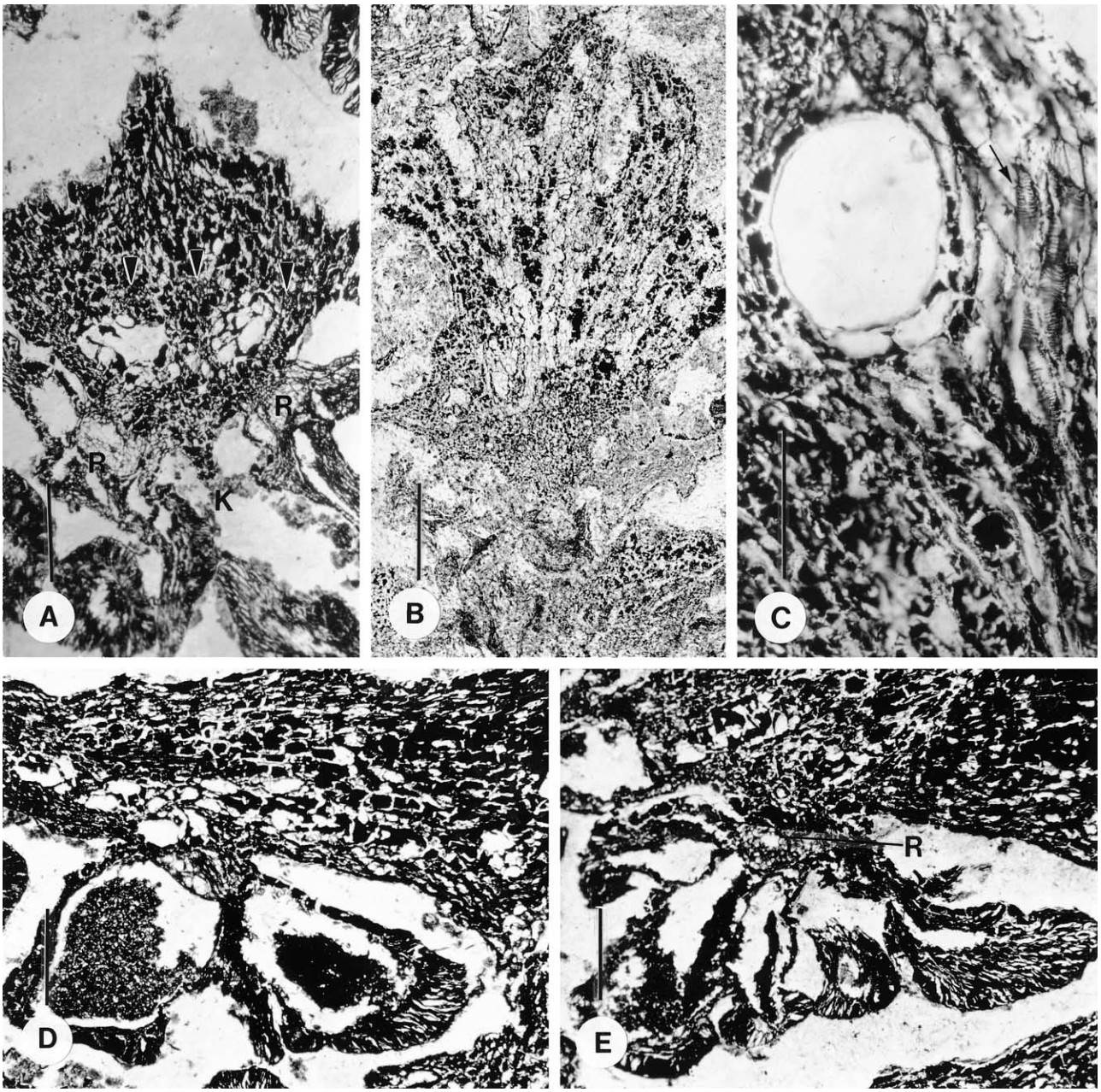

Fig. 2 *Delemaya spinulosa* gen. et sp. nov. *A*, Cross section through a microsporophyll with two clusters of pollen sacs on the abaxial surface separated by a sterile keel (*K*). Sessile pollen sacs are attached to parenchymatous, elevated receptacles (*R*); note also the ridges on the adaxial surface. Position of vascular bundles indicated by arrowheads. Scale bar = 250 μm. Slide 21438; 10424 M_{bot}, number 39. *B*, Paradermal section near the distal face of a microsporophyll, showing multiple adaxial projections. Scale bar = 500 μm. Slide 21439; 10424 L_{top}, number 25. *C*, Detail of cortical cavity and scalariform tracheids (arrow) in receptacle. Scale bar = 10 μm. Slide 21434; 10424 M_{bot}, number 115. *D*, Longitudinal section through a microsporophyll, showing two sessile pollen sacs attached to a parenchymatous receptacle. Scale bar = 250 μm. Slide 21440; 10424 M_{bot}, number 81. *E*, Longitudinal section through a microsporophyll, showing a cluster of five pollen sacs attached to the receptacle (*R*). Scale bar = 250 μm. Slide 21441; 10424 M_{bot}, number 67.

three vascular bundles enter the base of each microsporophyll (fig. 1*D*). Cells with opaque contents surround the vascular bundles and extend into the microsporophylls. Cells of the cortex are thin walled and isodiametric, like those in the pith. There are numerous hollow cavities present throughout the tissue (fig. 1*A*).

Microsporophylls

Microsporophylls are arranged helically on the cone axis, with imbricated rhomboid faces (fig. 4*A*) and wedge shaped in longitudinal section, with a slight abaxial keel and upturned apex (fig. 1*C*). Each microsporophyll measures up to 5 mm

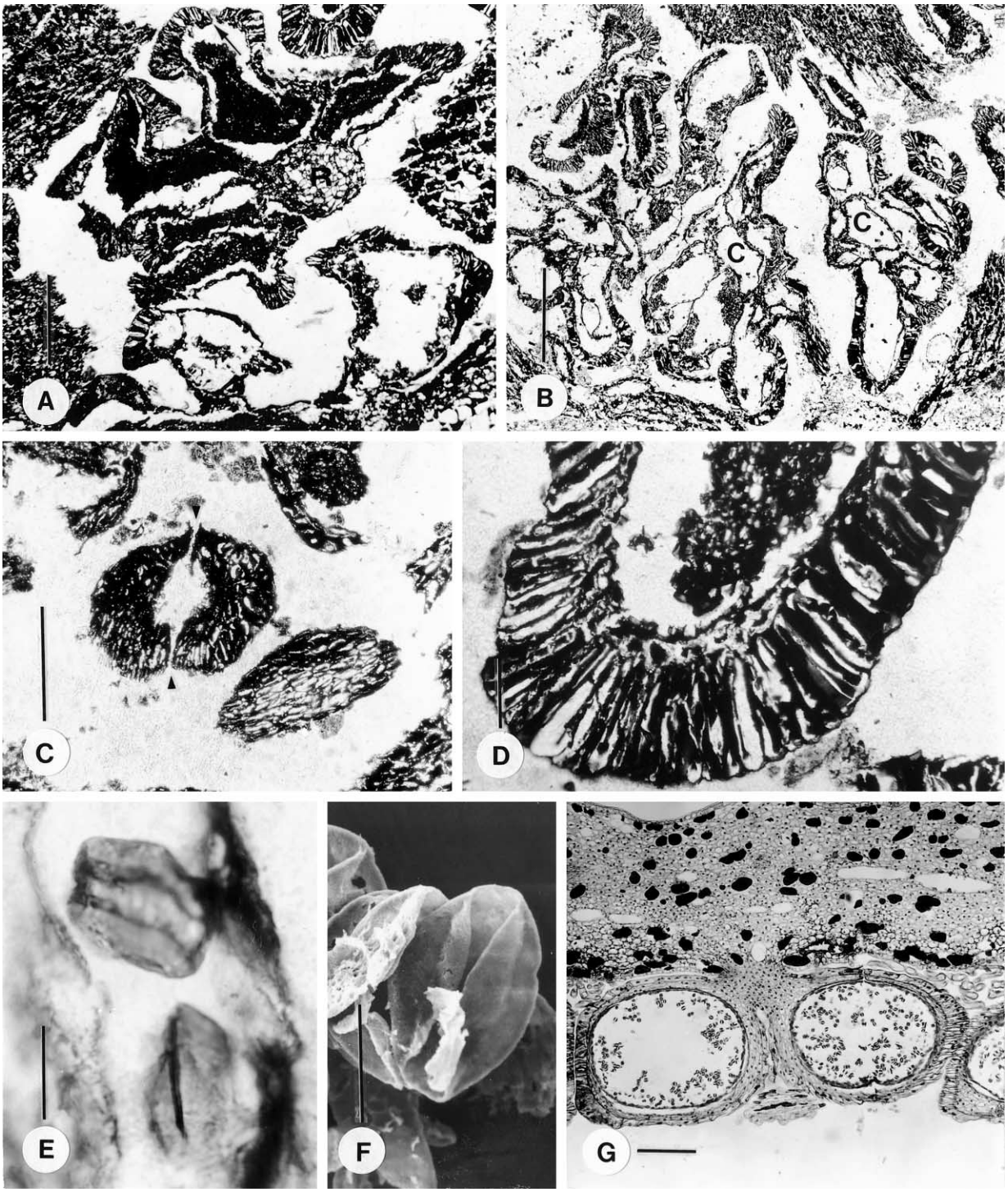

Fig. 3 *A–F*, *Delemaya spinulosa* gen. et sp. nov. *G*, *Zamia furfuracea*. *A*, Cross section through a single cluster of pollen sacs attached radially around the parenchymatous receptacle (*R*). Note dehiscence slit (arrow). Scale bar = 250 μm. Slide 21442; 10424 M_{bot}, number 68. *B*, Cross section through two radial clusters of pollen sacs that are attached to a single microsporophyll. Each cluster has five to six fused pollen sacs radially arranged around a central cavity (*C*). Scale bar = 500 μm. Slide 21443; 10424 M_{bot}, number 128. *C*, Paradermal section through two pollen sacs, on the left showing dehiscence zones on both sides of the pollen sac (arrowheads), and on the right showing elongate cells of the epidermis. Scale bar = 250 μm. Slide 21444; 10424 M_{bot}, number 69. *D*, Cross section through the wall of a pollen sac showing the multilayered structure with one to two layers of internal isodiametric cells and a single layer of rectangular epidermal cells. Scale bar = 5 μm. Slide 21444; 10424 M_{bot}, number 69. *E*, *In situ* pollen grains. Scale bar = 10 μm. Slide 21444; 10424 M_{bot}, number 69. *F*, SEM of pollen grains showing psilate surface and flared sulcus. Scale bar = 10 μm. *G*, Longitudinal section through a microsporophyll of *Z. furfuracea* with stalked, paired pollen sacs and cortical secretory cavity above point of attachment. Note also the multiseriate wall and increase in size of epidermal cells at the apex of the pollen sacs. Scale bar = 250 μm. NYBG V-91-01-H, 1–7.

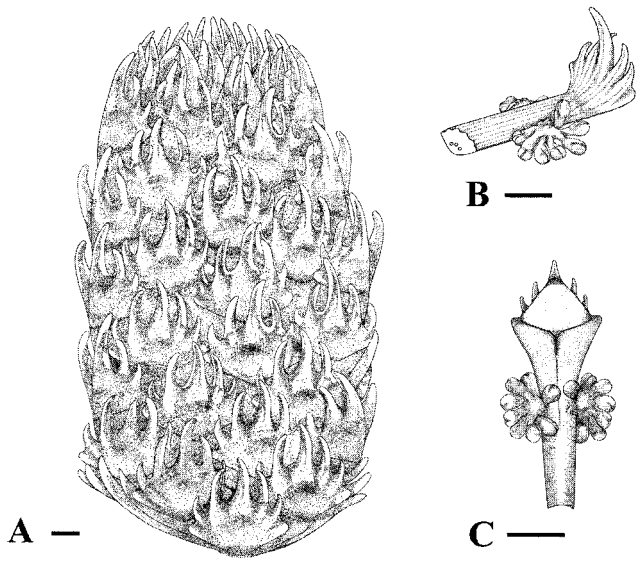

Fig. 4 Suggested reconstructions of *Delemaya spinulosa*. *A*, Cone morphology, showing helical arrangement of microsporophylls and organization of projections on microsporophyll faces. Scale bar = 1 mm. *B*, Morphology of a microsporophyll, showing the position of pollen sacs and extension of adaxial ridges into apical projections at the microsporophyll face. Scale bar = 2.5 mm. *C*, Abaxial view of a microsporophyll, showing the organization of the pollen sacs into two radial clusters. Scale bar = 2.5 mm.

long. Near the base, microsporophylls are rhomboidal to pentagonal in cross section, with a ridge on the adaxial (upper) surface, and measure 0.5 mm wide. Additional adaxial ridges appear in more distal regions of the sporophyll (fig. 2*A*) and extend to the upturned apex, where they expand into five sharp-tipped projections oriented toward the cone apex (fig. 2*B*). The middle projection is the longest (3.6 mm long at lower levels in the cone). The distal face of the microsporophylls is rhomboidal in overall shape and measures up to 4 mm wide. There is no evidence of trichomes or other epidermal outgrowths on any surface of the microsporophylls, nor have stomata been observed.

Three separate vascular bundles, composed of annular to scalariform tracheids (up to 24 μm in diameter), occur in the base of each sporophyll (fig. 1*E*). The two clusters of pollen sacs are vascularized by single strands that become continuous with the lateral bundles. A large (up to 250 μm) spherical cavity occurs in the receptacle of each cluster (fig. 2*C*). These cavities are empty and do not appear to have an epithelial lining. Similar structures also occur in modern *Zamia furfuracea* Aiton (fig. 3*G*). Additional cavities appear throughout the microsporophyll lamina (figs. 1*C*, 2*A*), but it is not clear whether these are secretory. Two of the vascular bundles divide distal to the point of attachment of the pollen sacs. As a result, the distal regions of the microsporophyll contain five vascular bundles in a curvilinear arrangement (fig. 2*A*, arrows). Bundles extend into the sharp-tipped projections that project from the face of the microsporophyll.

Pollen Sacs and Pollen

Microsporophylls bear from eight to 16 pollen sacs, which occur in two separate clusters positioned near the lateral margins on the abaxial surface of the sporophyll, approximately midway between the sporophyll face and the point of attachment to the cone axis (figs. 1*C*, 2*A*). Clusters of pollen sacs at the apex of the cone bear fewer pollen sacs than those below. A sterile region that forms a keel at the tip of the sporophyll separates the fertile regions (fig. 2*A*). Each cluster has up to eight pollen sacs organized radially; some are oriented with their distal tips toward the cone apex. Pollen sacs are sessile and broadly attached to a central parenchymatous receptacle that is slightly elevated from the abaxial surface of the microsporophyll (fig. 2*A*, 2*D*, 2*E*; fig. 3*A*). The receptacle is vascularized by tracheids with scalariform thickenings that extend throughout the parenchymatous pad (fig. 2*C*, arrow). Within a single cluster, pollen sacs are entirely fused to one another for up to half of their length, with their distal tips free (figs. 2*E*, 3*B*). Pollen sacs are elongate and measure up to 1 mm long and 0.5 mm wide. Dehiscence occurs by a single longitudinal slit that extends around the apex of the pollen sac (fig. 3*A*, 3*C*); as a result, pollen sacs open by two nearly equal valves (fig. 3*C*).

The pollen sac wall is multilayered, with two or three layers of small-diameter, thin-walled cells present beneath a distinct epidermis (fig. 3*D*). We are unable to determine whether the pollen sac walls are cutinized. The wall varies in thickness, reaching the greatest dimensions at the apex, where it measures up to 130 μm thick (fig. 3*B*). Epidermal cells are narrow, rectangular to nearly triangular in longitudinal section, and thick walled (fig. 3*D*). In paradermal view, these cells are elongate (fig. 3*C*). Where pollen sacs are fused, the wall is thin and individual cells indistinct (fig. 2*E*; fig. 3*A*, 3*B*). All pollen sacs in the cone appear to be at approximately the same level of development and contain mature pollen grains. Many sacs display a narrow opening on one or both sides and appear to have dehisced, although pollen frequently remains present. Pollen grains may be free but are more often aggregated into a compact mass, perhaps held together by remnants of a tapetal membrane (figs. 1*C*, 2*D*, 3*A*). This does not appear to be correlated with position in the cone and may instead be the result of taphonomic or diagenetic processes.

Pollen is ellipsoidal in outline, longitudinally monosulcate, and bilaterally symmetrical (fig. 3*E*, 3*F*). It appears to be similar to the dispersed pollen taxon *Cycadopites* Wodehouse ex L. R. Wilson et R. M. Webster. Individual grains range up to 15 μm wide and ca. 20 μm long. The sulcus occupies the length of the grain and is slitlike at the center, flaring up to 4 μm wide at the ends (fig. 3*F*). The surface is psilate, although numerous pits are visible in the surface of the grains. These are interpreted as the result of postdepositional degradation of the wall. Preliminary examination of ultrastructural thin sections suggests that the wall is homogeneous, with little indication of the alveolate structure found in modern cycad pollen grains. We are uncertain about whether the ultrastructure of the *Delemaya* pollen wall is, in fact, naturally homogeneous or is the result of extensive compression and the various diagenetic processes involved in preservation. We are currently

examining fine structural details of these grains; this information will be presented in a subsequent article.

Discussion

Among extant seed plants, conifers, taxads, and cycads can have microsporophylls organized into simple cones, and the overall structural organization of these cones may be similar (Bierhorst 1971). Cones in most of these groups have helically arranged microsporophylls and abaxial pollen sacs; however, whereas noncycad taxa typically bear ≤15 pollen sacs per microsporophyll, some species of cycads (e.g., *Cycas media* R. Brown) can bear >1000 (Chamberlain 1935; Bierhorst 1971). Conifer fossils assignable to the Podocarpaceae (*Notophytum krauselii* Meyer-Berthaud et Taylor) and Taxodiaceae (*Parasciatopitys aequata* Yao, Taylor et Taylor) have been discovered in the flora from Fremouw Peak (Meyer-Berthaud and Taylor 1991; Yao et al. 1997; Axsmith et al. 1998), which might indicate that this cone represents the pollen-producing structure of one of these taxa. Pollen cones of modern Podocarpaceae are characterized by having two pollen sacs per microsporophyll and bisaccate pollen (Bierhorst 1971), which differs significantly from *Delemaya*. In extant Taxodiaceae, pollen cones can bear up to 10 pollen sacs per microsporophyll and have inaperturate or monocolpate pollen (Aulenback and LePage 1998); however, pollen sacs are not organized in radial clusters. Comparisons with other Triassic conifers such as *Voltziostrobus* Grauvogel-Stamm and *Sertostrobus* Grauvogel-Stamm also reveal significant differences in that both *Voltziostrobus* and *Sertostrobus* bear pollen sacs on elongate pedicels on the adaxial surface of the microsporophyll (Grauvogel-Stamm 1969). Overall, the complement of characters in this fossil cone is distinctly cycadalean. The primary features that support this assignment are organization of pollen sacs into radial clusters (sometimes referred to as "sori") on microsporophylls; multiseriate organization of the pollen sac wall, with a thick-walled epidermal layer; and the presence of monosulcate, ellipsoidal pollen. Although there is a report of an anatomically preserved cycad pollen cone from the Carboniferous (Taylor 1968), subsequent studies have concluded that its affinities are uncertain (Taylor 1970; Taylor and Millay 1977). Thus, *Delemaya spinulosa* is the first fossil pollen cone that can unequivocally be assigned to the cycads on the basis of anatomical features.

Delemaya spinulosa occurs in close proximity to a stem of *Antarcticycas schopfii*, which is currently the only cycad known to occur in the permineralized peat found at Fremouw Peak (Taylor et al. 2000). This strengthens the possibility that it is the pollen cone of *A. schopfii*. There are, however, no histological features that provide further evidence for connection, nor are patterns of structural similarity in cone and stem anatomy well known even in modern cycads. In addition, all other cycad pollen cone taxa known to date are based on compression fossils, which bear a completely different complement of features and provide little basis for comparison. For these reasons, we have chosen to assign this cone to a new genus and species.

Although compressions of fossil cones attributed to the Cycadales have been known for >100 yr, their organization has been understood only in terms of general morphology and pollen structure (Hill 1990 and references therein). The gross morphological features of *D. spinulosa* (fig. 4*A*) support the prevailing view that early cycad pollen cones possessed an organization similar to that of modern cycads (Thomas and Harris 1960; Delevoryas and Hope 1971; Hill 1990; Krassilov et al. 1996); however, some of the structural characters in this cone are not otherwise known in the Cycadales. As such, it provides a critical suite of features that may be of systematic significance; these include patterns of microsporophyll vasculature, organization and arrangement of the pollen sacs, and microsporophyll morphology.

The cone axis vasculature consists of a eustele that is dissected into numerous individual bundles, the result of the production of a large number of helically arranged microsporophyll traces, which also occurs in pollen cones of both extant cycads and conifers (Scott 1897). In the fossil cone, two adjacent cauline bundles produce two trace bundles, a pattern also observed in *Zamia loddigesii* Miq.; however, only a single bundle is produced in the trace of *Bowenia spectabilis* Hook. (Worsdell 1898), and patterns of trace emission remain poorly known in other cycad taxa. In conifers as well, the range of variation in the pattern of trace emission to microsporophylls is not well known but typically appears to be a single bundle. In *Delemaya*, one of the two initial bundles of the microsporophyll trace divides so that three bundles enter the base of each microsporophyll; two of these subsequently bifurcate to produce at least five strands that extend into the distal projections. In modern cycads, the number of bundles entering the microsporophyll varies (Worsdell 1898) but does not appear to be correlated with total number of pollen sacs. Some species of *Cycas* L. bear >1000 pollen sacs with only a single vascular bundle documented as entering the base of microsporophylls (Thibout 1896), whereas *Zamia* L. typically bears <50 pollen sacs, and each sporophyll has three to six vascular bundles at the base (Worsdell 1898; Chamberlain 1935). It is not yet clear whether these features are taxonomically significant, and further investigation is needed.

The pattern of organization of vascular bundles in the microsporophyll appears to be consistent within genera and has been correlated with overall sporophyll morphology (Worsdell 1898; Stevenson 1990). Microsporophylls with a flattened lamina (e.g., *Cycas*, *Stangeria* T. Moore) display a linear arrangement of vascular bundles, while those with an expanded, peltate apex (e.g., *Zamia* L.) have a more complex, nonlinear, and three-dimensional arrangement in distal regions (cf. fig. 52 with fig. 55 in Stevenson 1990). Although the position of vascular bundles is often obscure in microsporophyll cross sections of *D. spinulosa* (e.g., fig. 2*A*), their almost linear arrangement supports the interpretation of the microsporophylls as flattened rather than peltate. These anatomical features demonstrate the overall similarity of the fossil cone to those of extant taxa; however, significant differences become more apparent in the arrangement and organization of pollen sacs on the microsporophyll. There is little information available to date on organization of pollen sacs in fossil cycads. Although the full range of variation in pollen cones of extant cycads has not been completely investigated in detail, differences nonetheless have been documented that are informative at the generic or familial level. Some of these include the number of pollen sacs per microsporophyll, number of pollen sacs in each

radial cluster, and degree of fusion of the pollen sac stalks (Stevenson 1990; Norstog and Nicholls 1997; Jones 2002; Whitelock 2002). These characters, generally not adequately preserved in compression fossils of cycad cones, are revealed in exquisite detail in the specimen from Fremouw Peak.

Delemaya spinulosa differs from its extant relatives with respect to the organization of pollen sacs, both in number of sacs per radial cluster and per microsporophyll and in the attachment and fusion of the pollen sacs. The fossil cone appears to bear up to eight pollen sacs in a single cluster (fig. 4*B*, 4*C*) and probably bore <20 pollen sacs per microsporophyll. In contrast, most modern cycads typically bear radial clusters comprised of no more than five pollen sacs and may have several hundred pollen sacs per microsporophyll; only *Chigua* D. W. Stevenson, *Zamia*, and *Bowenia* W. J. Hooker ex J. D. Hooker have ≤50 (table 1). Coulter and Chamberlain (1917) hypothesize that a large number of pollen is an ancestral character in cycads, whereas small numbers are derived. Both *Semionandra laxa* Krassilov et Bugdaeva, a putative cycad from the Lower Cretaceous of Russia (Krassilov and Bugdaeva 1988), and *D. spinulosa* possess a small number of pollen sacs, which indicates that this character has been present in the Cycadales since at least the early Mesozoic. Thus, Coulter and Chamberlain's hypothesis may not be entirely supported by evidence from the fossil record to date. Alternatively, a reduced number of pollen sacs per microsporophyll either may have evolved before the early Mesozoic or has had multiple origins in the Cycadales.

The pollen sacs of *D. spinulosa* structurally resemble those of modern cycads, particularly in sporangial wall organization. Walls of the pollen sacs are multilayered at maturity, a feature that distinguishes cycads from conifers and taxads (Coulter and Chamberlain 1917; Gifford and Foster 1989). Epidermal cells are narrow and elongate, with thickened walls, and increase in size at the apex of the pollen sac; this also occurs in extant cycads (cf. fig. 2*D* with fig. 3*G*). On the other hand, whereas pollen sacs of extant cycads have stalks and attach directly to the microsporophyll, pollen sacs in *D. spinulosa* are sessile and attach to a vascularized, receptacular pad of tissue on the abaxial surface of the microsporophyll. Moreover, the pollen sacs in an individual cluster are fused to one another for at least half of their length and thus may be interpreted as synangiate. Although Chamberlain (1935) states explicitly that pollen sacs in modern cycads are not synangiate, most taxa are now interpreted as showing some degree of fusion of pollen sac stalks (Bierhorst 1971; Stevenson 1990; Jones 2002). In addition, plurilocular structures have been reported in *Cycas* and Zamiaceae (particularly *Macrozamia* Miquel) (Bierhorst 1971; Stevenson 1990). Partly fused pollen sacs have also been described in the suggested cycads *Cycandra profusa* Krassilov, Delle et Vladimirova from the Upper Jurassic and *S. laxa* (Krassilov and Bugdaeva 1988; Krassilov et al. 1996). Synangial pollen organs are a characteristic feature of late Paleozoic pteridosperms, which have been suggested as cycad progenitors for more than a century (Worsdell 1896, 1906; Scott 1909). It is interesting to note that the broad attachment of the pollen sacs in each cluster to a raised, vascularized receptacle in *D. spinulosa* is also present in some Paleozoic pteridosperms (e.g., *Feraxotheca culcitaus* Millay et Taylor (Lyginopteridales) and *Idanothekion callistophytoides* (Stidd et Hall) Rothwell (Callistophytales) (Stidd and Hall 1970; Millay and Taylor 1977, 1979; Rothwell 1980).

The pollen of *D. spinulosa* (fig. 3*E*, 3*F*) closely resembles pollen of modern cycads, which is characterized as ellipsoidal, longitudinally monosulcate, and bilaterally symmetrical (Audran and Masure 1977; Dehgan and Dehgan 1988; Marshall et al. 1989). Pollen in *D. spinulosa* is comparable in size (average = 20 μm), although on the low end of the range for extant cycads (19–49 μm) (Dehgan and Dehgan 1988). In addition, psilate surface texture is not uncommon in cycads (Audran and Masure 1977; Dehgan and Dehgan 1988; Marshal et al. 1989). Although monosulcate pollen is characteristic of cycads, similar pollen morphology can be found in extant and fossil *Ginkgo*; however, organization of the *Ginkgo* pollen cone differs significantly from that of *Delemaya*. Although the pollen sac organization of *D. spinulosa* differs somewhat from that of modern cycad pollen cones, pollen morphology strongly affiliates it with the Cycadales.

Cone Morphology

The anatomical features present in *D. spinulosa* also provide an increased understanding of overall cone morphology. The cone appears to be ellipsoidal in outline, with the tips of the microsporophylls imbricate (fig. 4*A*). In comparison with most modern taxa, the cone is relatively small. This may be related to the suggested slender stature of its possible parent plant, *A. schopfii* (Smoot et al. 1985). The size of the fossil cone is, however, comparable to several species of *Androstrobus* Schimper (Thomas and Harris 1961) and pollen cones of some extant taxa (e.g., *Zamia pygmaea* Sims; Whitelock 2002). The small size of the cone could also be interpreted as representing an early stage of development. In modern cycads, microsporophylls remain tightly appressed until maturity, when the cone axis elongates by increase in cell length, which results in separation of the microsporophylls and exposure of the pollen sacs. With additional space between microsporophylls, pollen sacs continue to mature and may show evidence of ontogenetic distortion that reflects crowding during development (Bierhorst 1971). In this specimen, however, the cone axis appears to have initiated elongation because the apical microsporophylls show slight separation, pollen sacs are mature and some are dehisced, and pollen grains are free (figs. 1*A*, 2*D*, 3*E*). The varied orientation of the pollen sacs (fig. 1*A*) indicates ontogenetic distortion and/or crowding the pollen sacs, similar to that in modern cycads. This combination of features indicates that the cone was preserved at or close to maturity and thus that it was compact relative to modern cycad cones. Because we remain uncertain about the overall length of the cone, it is possible that our interpretation of few pollen sacs per microsporophyll simply reflects better preservation of the apical region of the fossil cone. Chamberlain (1935) notes that microsporophylls near the apex of many cones bear a reduced number of pollen sacs, with some taxa displaying completely sterile apical microsporophylls. In *D. spinulosa*, however, the apical microsporophylls are fertile. In addition, proximal microsporophylls also appear to bear only two clusters of pollen sacs. This tends to support the hypothesis that a low number of pollen sacs per microsporophyll was the norm in *D. spinulosa*.

Table 1

Comparison of Features of *Delemaya spinulosa* and Modern Cycad Pollen Cones

		Cycadaceae	Stangeriaceae		Zamiaceae							
					Zamieae			Ceratozamieae	Encephalarteae			Diooeae
	Delemaya	*Cycas*	*Stangeria*	*Bowenia*	*Zamia*	*Chigua*	*Microcycas*	*Ceratozamia*	*Encephalartos*	*Macrozamia*	*Lepidozamia*	*Dioon*
Microsporophyll face shape	Rhomboid	Rhomboid	Rhomboid	Hexagon	Hexagon	Hexagon	Hexagon	Hexagon	Rhomboid	Rhomboid	Rhomboid	Rhomboid
Microsporophyll arrangement	Imbricate	Imbricate	Imbricate	Vertical rows	Vertical rows	Vertical rows	Vertical rows	Vertical rows	Imbricate	Imbricate	Imbricate	Imbricate
Distal face projections	At least five sharp spines, central spine longest	± single sharp spine projecting apically, some with one to six minute teeth to either side[a]	Flat	Central depression	Flat to faceted	Flat to faceted	Faceted with central facet projecting to a blunt tip	Two spines	Faceted with central facet often projecting to a blunt tip[b]	Terminal sharp spine	Apex inflated, tip extends in a single spine[c]	Top of face projects slightly
Pollen sacs/microsporophyll	<20	>700	>150	>50	<25	?	>200	>150	500–700	>500	>300	200–800
Pollen sacs/sorus	Up to 8	2–4	2–5	2–5	Usually 2	?	2–5	2–5	2–5	2–5	2–5	2–5

Sources. Compiled from Chamberlain (1935); Stevenson (1990); Norstog and Nicholls (1997); Jones (2002); Whitelock (2002).

[a] Length and orientation of spine(s) can vary from base to apex of cone; may be curved backward or downward.

[b] Lower edge of central or lower facet may be toothed or scalloped.

[c] Spine may be reduced at the base of the cone, more elongate toward the apex.

A curious feature of the microsporophylls is the morphology of the distal face (fig. 4*A*, 4*B*). There appear to be at least two morphotypes in fossil cycadalean cones reported to date. Although no fossil cone has yet been identified with peltate microsporophylls, fossil cycad cones can be distinguished on the basis of the presence or absence of projections on the distal face of microsporophylls. Cones assigned to the genus *Androstrobus* do not display significant projections on the sporophyll face (Schimper 1870–1872). In contrast, spinelike distal projections have been described in *Liulinia lacinulata* Wang from the uppermost Permian of China, although the numerous projections on this compression specimen are interpreted as blunt (Wang 1986). Microsporophylls of the cone of *Leptocycas gracilis* Delevoryas et Hope from the Upper Triassic of North America also have elongate apical projections (Delevoryas and Hope 1971). Reexamination of the type material of *L. gracilis* reveals that microsporophylls have at least one sharp-tipped projection at the distal face that extends laterally up to 5 mm. Although this feature alone is not a definitive basis for establishing relationships among early cycads, variation in microsporophyll morphology is a character that is taxonomically informative at the generic level in extant taxa (Stevenson 1990; Norstog and Nicholls 1997; Jones 2002; Whitelock 2002). Where present, these projections range from the beaklike extension of a central facet of the face in *Encephalartos* Lehmann to two well-defined spines in *Ceratozamia* Brongniart to a single spine, sometimes with minute spines on either side, in many species of *Cycas* (table 1) (Jones 2002; Whitelock 2002). As more is learned about sporophyll morphology in fossil cycad cones, this feature may become more important in defining taxonomic lineages.

The arrangement of the face of the microsporophylls is another feature that is consistent within taxonomic groups of modern cycads. All extant taxa bear microsporophylls in a helical arrangement, but this can manifest as two different patterns of organization on the basis of the shape of the microsporophyll face. Cones of Cycadaceae and some Zamiaceae (Encephalartae and Diooaeae) display an imbricating spiral of rhomboidal faces, while those in Stangeriaceae and other Zamiaceae (Zamieae and Ceratozamieae) have vertical rows of hexagonal faces (table 1). All fossil cycad cones known to date, including *D. spinulosa*, display an imbricating arrangement of microsporophylls with rhomboidal faces (fig. 4*A*).

Fossil Record of Cycad Pollen Cones

Cycads are believed to have originated during the late Paleozoic, possibly during the Carboniferous (Scott 1897; Worsdell 1906; Mamay 1976; Taylor and Taylor 1993), although much of the fossil evidence for this hypothesis is equivocal. Whereas there are numerous Late Carboniferous–Early Permian leaf compressions that have been assigned to the cycads (e.g., *Taeniopteris* Brongniart, *Archaeocycas* Mamay, and *Phasmatocycas* Mamay; Mamay 1973, 1976), there are few reports of cycad reproductive structures. *Lasiostrobus polysacci* Taylor was originally described as a cycad (Taylor 1968) but later compared with cycads, conifers, and ginkgophytes (Taylor 1970). Today, this fossil's correct taxonomic placement remains an enigma (Taylor and Millay 1977). Hu et al. (1999*a*) briefly describe ovulate cycad sporophylls from the Upper Carboniferous in China; however, this occurrence has not yet been documented in greater detail. Other fossils suggested as cycads include impressions and molds of conelike structures from the Lower Permian of Texas and an isolated megasporophyll assigned to *Cycadospadix* Schimper (Mamay 1976). The most convincing evidence to date of the presence of cycads in the late Paleozoic comes from the Permian of China and includes compression specimens of leaves, ovulate megasporophylls, and pollen cones (Zhu and Du 1981; Wang 1986; Gao and Thomas 1989; Zhu et al. 1994; Hu et al. 1999*a*, 1999*b*; Liu and Yao 2002). These fossils provide compelling evidence for strobilar organization in both pollen and seed-bearing reproductive organs in the latest Paleozoic cycads and support the hypothesis that ancestors of cycads may date to the Carboniferous.

The fossil record of cycads in the Mesozoic is more complete but complicated by similarities in vegetative structure of cycads and Bennettitales (cycadeoids). There are numerous reports of fossil cycad leaves and stems (review in Norstog and Nicholls 1997), yet reproductive structures remain poorly known or inaccurately identified. Most fossil cones suggested as belonging to cycads occur in isolation, although a single pollen cone has been found attached to the apex of a stem of *L. gracilis* (Delevoryas and Hope 1971). The cone is ca. 6 cm long and 1.5 cm wide, but additional details of its structure are not well preserved. The pollen cones *C. profusa* from the Jurassic of Georgia and *S. laxa* from the Cretaceous of Russia (Krassilov and Bugdaeva 1988; Krassilov et al. 1996) provide some evidence of diversity in Mesozoic cycads. Many other putative cycad cones have been assigned to *Androstrobus*, with at least 16 species described from Upper Triassic–Cretaceous localities in Europe and China (Schimper 1870; Saporta 1875; Heer 1876; Nathorst 1878; Seward 1895; Harris 1941, 1964; Stanislavski 1957; Roselt 1960; Thomas and Harris 1960; van Konijnenburg-van Cittert 1968, 1993; Hill 1990; Hu et al. 1999*b*). Although cycadalean pollen has been identified in some of these species (Harris 1941; van Konijnenburg-van Cittert 1968, 1993; Hill 1990), the validity of assignment of others to the Cycadales is questionable, and revision of *Androstrobus* is sorely needed (Harris 1964). Cones of *Androstrobus* range up to 7 cm long and are characterized by imbricating microsporophylls that lack distal projections (Schimper 1870; van Konijnenburg-van Cittert 1968). Hill (1990) suggests that *Androstrobus* most closely resembles cones of extant Zamiaceae; however, this sheds little light on familial affinities because characters of pollen cones in Zamiaceae *sensu* Stevenson 1990 encompass nearly all of the variation that occurs in cycads (table 1).

Systematic Considerations

The cycadophytes (Cycadales and Bennettitales) were significant elements of many Mesozoic ecosystems worldwide but today are represented by only one order that is comprised of 11 genera and ca. 300 species (Jones 2002; Whitelock 2002). Extant Cycadales include three families: Cycadaceae, Zamiaceae, and Stangeriaceae (Stevenson 1990, 1992). Cycadaceae, with the single genus *Cycas*, has historically been interpreted as the most basal family, and this is supported in recent phylogenetic analyses (Stevenson 1990; Caputo et al. 1991; Nixon

et al. 1994; Rydin et al. 2002; Treutlein and Wink 2002). Zamiaceae is consistently regarded as the most derived, although relationships among the eight genera included in the family remain unresolved (Crane 1988; Stevenson 1990; Treutlein and Wink 2002). The monophyly of Stangeriaceae (*Stangeria* + *Bowenia*) has recently been challenged on the basis of molecular and cytological studies, and it appears that *Stangeria* may be more closely related to *Zamia* than to *Bowenia* (Kokubugata et al. 2002; Treutlein and Wink 2002; Bogler and Francisco-Ortega, in press; Rai et al. 2003). Nearly all phylogenetic analyses of seed plants based on morphology score cycads on the basis of characters of the extant taxa; only a few include any fossil representatives of the order (Doyle and Donoghue 1986, 1992; Doyle 1996). Assessment of possible systematic affinities and phylogenetic relationships of fossil cycads has been limited, in part because of the lack of detailed information on reproductive structures but also because phylogenetic analyses have used characters that either cannot be ascertained (e.g., presence of cycasin) or have not been used in fossil taxa (e.g., trichome characteristics) (Crane 1985, 1988; Stevenson 1990). In addition, these analyses generally use a limited suite of cycad morphological and anatomical features, particularly with respect to pollen cones. With the exception of the work of Stevenson (1980*a*, 1980*b*, 1981, 1988, 1990), this is probably a reflection of nearly a century of neglect in detailed anatomical and developmental studies of extant cycads.

In their description of *A. schopfii*, Smoot et al. (1985) are cautious in assigning the fossil to a modern cycad family and suggest tentative affinities with Stangeriaceae/Zamiaceae on the basis of the observation that its anatomical organization is similar to that of *Bowenia*. Some of the features of *Delemaya* are more similar to pollen cones of *Cycas* (Cycadaceae) and *Macrozamia* (Zamiaceae), which have imbricating, planar microsporophylls with one or more distal spines; however, *Zamia*, *Chigua*, and *Bowenia* are all characterized by a reduced number of pollen sacs per microsporophyll (table 1). Nonetheless, sufficient differences separate *D. spinulosa* from these taxa, including the extremely reduced number of pollen sacs per microsporophyll (ca. 16 vs. 50–1000 or more), greater number of pollen sacs per radial cluster (up to eight vs. up to five), and synangiate organization of the pollen sacs. On the basis of *rbc*L sequence data, Treutlein and Wink (2002) suggest that the split between Cycadaceae and Zamiaceae occurred in the late Mesozoic, with a relatively recent radiation of most extant species of cycads. If this hypothesis is accurate, it is perhaps not surprising that this early Mesozoic pollen cone appears to possess characters of both Cycadaceae and Zamiaceae as well as features that are unique. We believe that these characters must be interpreted with caution because *D. spinulosa* is thus far known from an isolated, single specimen, which does not provide information on the full range of variation that no doubt existed. The unique characters of this pollen cone, however, when examined with the anatomical features of the cycad stem *A. schopfii*, suggest that assignment to a modern cycad family is perhaps premature at this time.

Pollination Biology

Delemaya spinulosa is a small cone with a reduced number of pollen sacs and therefore lower pollen production when compared with the pollen cones of modern cycads (Norstog and Nicholls 1997). This raises the question about how pollination was achieved in this early cycad. One method to compensate for a relatively low pollen output is for the plant to have produced multiple cones, possibly on multiple stems. This strategy is employed by several modern genera; *Zamia* can produce more than a dozen cones on a single stem, while multibranched *Macrozamia* has been documented with up to 100 pollen cones (Chamberlain 1935; Norstog and Nicholls 1997). The small size of stems of *A. schopfii* (<4 cm in diameter), the probable parent plant, would seem to preclude the production of many cones at one time, but it remains possible that it had a branching habit.

On the basis of what we now know about pollination mechanisms in modern cycads, it is possible to envision that this fossil cycad may have attracted insects that acted as a vector for a more sophisticated, directed, biotic pollination syndrome. It has become increasingly clear that most, if not all, modern cycads depend on insect pollinators (Norstog et al. 1986; Tang 1987; Norstog and Fawcett 1989; Vovides 1991; Donaldson 1997; Norstog and Nicholls 1997; Stevenson et al. 1998; Mound and Terry 2001; Terry 2001; Jones 2002). Members of the insect groups that act as pollinators in modern cycads were present in terrestrial environments by the Triassic (Labandeira and Sepkoski 1993), and it has repeatedly been hypothesized that the history of mutual relationships between cycads and insects may date back to the Mesozoic or possibly earlier (Norstog 1987; Norstog and Nicholls 1997; Labandeira 1998; Mound and Terry 2001; Schneider et al. 2002). Indirect evidence for this is provided by isolated cycad pollen sacs containing coprolites that consist exclusively of cycad pollen that occur in association with this cone. This may simply be an instance of opportunistic predation; however, pollinivory has been hypothesized as one of the early steps in establishing such an interaction (Crepet 1979; Labandeira 1998). Research on these intriguing fossils continues.

Renewed interest in the evolutionary history of cycads has been triggered by the discovery of exciting fossils in China as well as recent phylogenetic investigations using molecular data. Nonetheless, interrelationships within the cycadophytes remain poorly understood, as does their phylogenetic position relative to other seed plants. This can be attributed in part to the few reports of fossil cycad reproductive structures. Our understanding of even the living cycads remains in its infancy when measured against the wealth of information that has been gathered for other gymnosperms. The discovery of *D. spinulosa* from the Middle Triassic of Antarctica presents another perspective on the reproductive biology of fossil cycads. This ultimately may provide a new impetus for incorporating fossil cycad taxa into phylogenetic analyses and contribute to a more complete understanding of the evolutionary history of this extraordinary group of seed plants.

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